This paper is part of the theme edition of *Australian Zoologist* - "Dangerous Ideas in Zoology"

10 Possible Limitations of Current Ecological Theory

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ABSTRACT

I make ten observations of the limitations of ecological science as I have seen it develop over the last 56 years. The key focus is on the scientific maturity of our approaches, and the constraints that flow from pretending we are physicists, that progress will come from more mathematical models, and that generality will flow from short-term studies. All of my observations may be incorrect but they might generate some useful discussion about dangerous ideas on where ecology is headed.

Key words: population ecology, community ecology, conservation, mathematical models, generality, ecological theory, climate change, meta-analyses

DOI: http://dx.doi.org/10.7882/AZ.2014.032

Introduction and Discussion

From 56 years of observing, reading, and writing about ecology, I list here some of the concerns I have about the current state of ecology in 2013. I do not pretend that these observations are correct or profound, but they do seem to me to be worth thinking about and discussing. As with all observations, they are filled with weasel words, since 'all' is rarely correct and 'most' or even 'some' might be more precise. And, as always, remember that age and wisdom are only loosely correlated.

Why should we be worried about dangerous ideas? I think any scientific concerns would be classified as dangerous ideas even if they are only partially correct because they may point out distortions that impede progress in ecological understanding. In a complex science like ecology there is never one clear path to understanding and a continued discussion of the current fads in ecology is important as is a discussion of possible dangerous ideas. The history of science is peppered with dangerous ideas that were later found to be the quintessence of truth.

I should be precise about what I discuss here. First of all, I am considering ecology with respect to understanding the reasons for the *distribution and abundance* of organisms, and thus the reasons why distribution and abundance should change. I am not discussing behavioural ecology, physiological ecology, evolutionary ecology, or descriptive ecology except insofar as these disciplines attempt to develop explanations for changes in distribution and abundance. Each of these disciplines has its own problems that are not necessarily covered here. Secondly, ecology in the broad sense can be subdivided into *political ecology* and *scientific ecology*. Political ecology has two foci. First, it is a form of advocacy for good conservation management, proper regulations for the management of exploited populations and environmental protection in the broad sense. A second form of political ecology is the attempt to convince the powers-that-be to provide adequate funding for scientific ecology. Political ecology is most difficult because too many people seem to view the environment as a garbage can and the value of biodiversity only in dollars. In political ecology, as in modern medicine, one achieves the goal of obtaining more funding by overpromising significant results that will arrive next year or appealing to imminent catastrophe. Political ecology is a very important activity but here I deal only with scientific ecology.

Scientific ecology does not have a strong single focus because ecologists are not sure what model of science to follow. The dominant model followed in many sciences is that of physics, strong mathematical models, ruthless tests of hypotheses, universal explanations producing laws of nature. Another model adopted is that of the social sciences - weak inference, probability models, low predictive power, often associated with the view that every ecosystem can operate under different rules (subject of course to the laws of physics). A third model of ecology might be called the 'review model' and operates with the maxim 'stay at your desk and gather papers for an overview'. This is an important model for ecology but can be overused if not balanced with data acquisition. Evolution has produced yet a fourth model that some ecologists favor - post-hoc explanations with many exceptions that can be safely ignored, no predictive power, and endless descriptions with the hope that wisdom will emerge from gene sequences. Lastly, there is the natural history model of ecology which ignores all theory and argues we are too short of adequate descriptive data to say anything general about the earth's ecosystems. There are many subspecies of these five oversimplified models of ecological science, but the differences between these five paradigms are so large that they do not cross communicate very well, with the resulting mess that I think typifies our science at present. I attempt to summarize the major reasons for our current chaos in ecology in the following ten limitations to our current science. These ten limitations can be viewed as dangerous ideas if they are deflecting ecological progress into blind alleys.

1. Most ecological theory is poorly formulated and poorly tested. Distrust every sentence that begins with 'Ecological theory predicts that...'

There is of course a problem of agreement on what is meant by 'ecological theory'. I use it here to define the physics model of ecology. There is some discussion about defining the 'principles' of ecology (Berryman 2003, Braysher et al. 2013, Scheiner and Willig 2008, 2011). Theories might more correctly be called 'hypotheses' in ecology. If there is not at least one alternative hypothesis, the hypothesis under investigation is usually a fraud. If a hypothesis can be answered with a 'yes' or 'no' it is typically trivial. If it is a null hypothesis, we can be sure it is not correct. If a hypothesis makes only general predictions it can be useful but would be more useful if it were quantitative and precise.

In spite of this admonition, there are broad ecological generalizations that are worthy of discussion and further investigation. One does not know what to make of statements like "Diversity leads to stability" in ecosystems. If this is a theory that is a good fit to a majority of our communities and ecosystems, what do we make of a study that does not support this theory? It is probably better to consider it a hypothesis or a verbal model than to call it a theory. It is hardly rigorous enough to form the basis of conservation management, although it is often used in such a way. I think it is an interesting idea, but not very rigorous as one might like. Often the utility of such ideas is that they promote discussion. But if we use such ideas to make judgments in management we should be careful about what they imply. The best advice for budding ecologists is to "seek generality but distrust it".

2. Populations can usually be defined and studied, communities can rarely be, and ecosystems are impossible to define or limit. The result is endless description after the fact.

All of science proceeds on the assumption that units of some type can be defined but in ecology particularly at the higher levels the world is a continuum.. In general, biology has no problem defining individuals as units. Populations are somewhat vague as to their limits, but population ecologists recognize this by including immigration and emigration in their studies. Communities on the other hand are more difficult to put boundaries to. We can use vegetation types as a unit of study, but they may be irrelevant to many of the organisms that use a particular vegetation type. A food web approach attempts to make an operational definition of a community of interacting species, but many of the species in the food web do not interact, so typically we use a partial food web that includes only the species of interest, typically the larger vertebrates or charismatic species like butterflies, or the valuable species such as harvested marine fishes. One of the descriptive agendas of modern ecology is to show that species have indirect connections that affect numbers or geographic range through mechanisms such as apparent competition and trophic cascades. Community ecology typically fails because it has no quantitative arithmetic, and the nonsense multivariate statistical plots we are continually exposed to are a typical sign of desperation in explanation by confusion. Recognizing patterns is a useful starting point for community studies but it is the processes that are critical for understanding.

Ecosystems are yet one further step into talking about vague units, since one can talk about the ecosystem of a city park, of Serengeti National Park, of an island like Ireland, or of all of Australia. So ecosystems are units of convenience whose replication is quite impossible because for large ecosystems their evolutionary history differs. The consequence is that ecosystem ecology collapses into descriptive natural history or political ecology about 'ecosystem services'. Those roles are not unimportant but indicate that ecosystem ecology has not yet matured as an area of robust science. Except for nutrient cycling and the laws of physics, there is no arithmetic of ecosystems to guide our studies into these complex systems.

3. Most ecological modeling is elegant, unrealistic, and untestable. It is relatively harmless as long as you do not believe its conclusions.

Mathematical modeling is the epitome of theoretical ecology and can be a saviour or a curse for the development of the science of ecology. It is based on physics envy, and on the premise that by simplifying a system you can determine its structural core. At best it achieves some of this goal in population ecology, largely because there is an arithmetic of populations that is well developed. But once it moves to model food web dynamics or community dynamics it becomes more of a hindrance than a help. The beauty of physics has always been that it alternated between models and measurements, but most ecological models have variables that are empirically impossible to measure so they are rightfully ignored by practical ecologists interested in how the real world works.

Ecology has progressed in the last 60 years to more and more complex models that are more and more useless. The difficulty has been that a complex model can be formulated in a time frame of days to weeks while the field studies relevant to testing that model can be carried out only in a time frame of years to decades. The assumptions of any particular model and its predictions are often poorly articulated.

Nevertheless perhaps because of mathematics- or physics-envy, ecologists have elevated modelers to be the high priests of our science. To be clever in mathematics is an admirable skill but whether it benefits the advance of our ecological understanding can certainly be questioned.

4. Past ecological generalizations are rapidly becoming unreliable because of human changes to the biosphere. The ecology of the human-dominated earth will be unrecognizable to older ecologists.

There is an enormous difference in ecological conferences held in Europe, New Zealand, and Australia, and those held in North America. The hand of mankind is not kind to ecologists, and our job in many countries is to try to sort out the ecological messes left by forestry, industrial agriculture, mining, and urban intensification. Some ecologists study relatively pristine systems, the ecology of pristine systems is almost completely irrelevant to solving the environmental problems of today. The loss of trophic cascades because of the extermination of top predators is a clear example (Estes et al, 2011). The extremely intractable problem of invasive species arising from poor land management is perhaps the most serious practical ecological issue of our time. Our response to invasive species is too often "Poison is the answer, now what is the question?. Poisons can be useful in management, but they are best a short term solution.

Additions and subtractions from food webs have released a cascade of problems we cannot anticipate because we have such a poor understanding of most food webs. By releasing an array of herbivores and omnivores from top predators, or by adding a top predator to a food web, we have rendered the normal 'pristine' understanding of species interactions irrelevant. Thus we have issues with superabundant deer in eastern North America, and species extinctions in Australia. These are problems ecologists are expected to solve without re-establishing the former trophic structure. Re-wilding will not work when people will not tolerate wolves in New York City.

Our situation in this regard is similar to that of the medical profession who must deal now with obesity, smoking, drug use, new pathogens, and chemical poisons from air pollution and industrial agriculture, all of which generate new diseases for which people demand treatment. The difference in the developed world is that money flows to medical science in large amounts, but much less to ecological science caught in the same dilemmas.

5. Conservation ecology is of great practical importance but is a hypothesis-free-science with many after-the-fact descriptions, little hard data, much speculation and unreachable goals.

Reading the conservation literature is an exercise producing depression, 2 success stories followed by 14 disasters. The science of conservation is applied ecology with many constraints that prevent proper scientific study. There is no time for hypothesis testing or the niceties of scientific inference. The problem is how to deal with rare and declining species. The answer is to set aside nature reserves of large size, connected if possible and put the large animals in zoos. So, for the most part, conservation ecology is political ecology and relies on wishful thinking.

The problem ecologically is that most species are rare, and as far as we can tell this has always been the case in the fossil record. And rare species are nearly impossible to study for the simple reason they cannot be counted easily. They can be put on the Red List of IUCN or listed as Species at Risk in some countries but if there are few data on their ecology, there is no ecological understanding of why they are rare. The category of species that were once common and are now declining is different if we know the reasons for their decline. In many cases it is overharvesting for valuable byproducts or meat, or habitat loss due to human expansion. In these cases some controls might be applied, but poverty and the need for agricultural expansion to feed the growing human population often blunt any action in developing countries. The goalposts of conservation are continually shifting. In some cases they are shifting in the direction of success, in other cases not. But the long-term prognosis is dim, and conservation ecology resembles too much the Emergency Ward of a hospital in a large city. This is no reason not to work for conservation which we all recognize is very important, but a general scientific approach to conservation problems cannot be expected. The devil remains in the details.

6. Conservation genetics and ecological genetics provide useful biogeography but little insight into future conservation needs or evolutionary trends.

Given the frustrations of conservation ecology and the successes of modern genetics, many conservation biologists have turned to conservation genetics as a way of avoiding depression. Given that we can run sequences in a few hours, and generate many bytes of data, there must be some questions we can answer that will assist conservation biology. The results are a mixed blessing. For biogeography, we can obtain much interesting and more precise inferences of faunal origins. For investigations of population structure and microevolution, we obtain much more precision. But the past is not necessarily a good guide to the future. For conservation the only positive I can see from the new genetics is the ability of elevate every subspecies to the species level, thereby increasing biodiversity without anything changing in the real world.

Let us admit that modern genetics can map evolutionary trends, so that for example we can ask if there is adaptation to rising temperatures. The problem is that the evolutionary trends we can map could be temporary or stochastic, and are unlikely to permit any prediction of long-term trends. Other genetic advances such as bar-coding for species recognition can be useful if expensive ways to gather more biodiversity data in a hypothesis-free manner. A list of conservation genetic hypotheses that are scientifically testable would be very short, and we persist with broad generalizations about genetic variability that are rarely of use to conservation managers.

7. Most ecological studies are too short to provide any insight into trends, and do not provide the background for expected changes. The three-year-PhD study should not be the ultimate standard for ecological analysis.

The key question many ecologists now ask is what should be the temporal unit of study. For most published papers, the time frame is 2-3 years. This is dictated by the universities' PhD programs and by government funding which is short term and short sighted. We can say then that we have no choice in this matter, but we do. We can support long-term studies as a critical test of the common assumption of a static world, or if you prefer, of the hypothesis that climate change is not affecting the system under study.

Long-term studies are only part of a solution to this deficiency, since without good hypothesis testing, long-term studies are compromised. There is considerable discussion of how monitoring studies should be organized (Nichols and Williams 2006, Lindenmayer and Likens 2009). Clearly the optimum arrangement is for monitoring to be designed as hypothesis-testing, but monitoring in a hypothesis-free world has the potential to be useful in future for things we cannot anticipate. The problem as always is funding. Governments in general have not looked with favor on monitoring unless they can see a practical utility for it (Would it be useful to reduce bear attacks on people? Would it give guidance to oil tankers traversing arctic ice?).

The opposite question of how long should long-term studies continue before they are terminated has not yet come to the fore. In ecology most long-term studies are terminated by the retirement of the ecological advocate, but this is clearly not an optimal solution. The key question is always the simple one - is this study providing key insights as new problems arise and new techniques can be utilized? Or is it just repeating the same data message? Of course, society has decided that some monitoring programs like the weather and the stock market are to continue forever regardless of how useful the data are. I doubt that ecological monitoring will be given such a kind evaluation.

8. Climate change can explain everything if you are interested only in after-the-fact correlations and speculation. Most ecological systems have so little background data that trends cannot be separated from normal fluctuations.

We are in the midst of extensive discussions of climate change, and since ecologists wish to be relevant, they now tend to slant their research toward the consequences of climate change for population X or community Y. Climate change must be a key word in all grant applications and graduate proposals. So the paradigm is simple: measure something ecological that is changing (or get some old data), do a sophisticated statistical analysis with every weather variable you can get data on, calculate AIC(c) values, publish quickly, and never get later data to test the resulting model. I suspect that nearly all of the resulting analyses are based on spurious correlations for the reasons that statisticians have been pointing out for at least 60 years. So one has to repeat endlessly the mantra that 'correlations are not causations'. The temptation to do this is overwhelming because in general it is impossible to manipulate weather to test any hypothesis in an acceptable manner, and the only solution is to wait-and-see (not a good career move for young scientists) or to pretend that statistics delivers truth.

These kinds of climate data analyses also raise the glass-half-full dilemma that is illustrated in nearly every empirical paper in our journals. Suppose you test some mechanism and produce a graph that has a correlation between some weather variables and your ecological measure of say $r = 0.7$, or $R^2 = 0.49$. The statistician tells you this is highly statistically significant. The question is then: should you be ecstatic with your success of explaining statistically 49% of the variation, or should you be totally depressed that you have 51% of the variation unexplained? If you are young, you accept option 1; if you are old and jaded you look more favorably at option 2. And in both cases you say that more study is needed, which is certainly correct.

9. One good experiment is worth 10 meta-analyses. Wisdom does not emerge from 100 poorly designed short-term studies.

In ecology we are in the era of meta-analyses, and the general advice one can give to young ecologists is to get on a team that generates meta-analyses if you wish to get a job. The key question is whether any science advances by meta-analyses. I doubt that any does, but I am sure I am in a minority on this issue. Virtually every meta-analysis I have examined in SCIENCE or NATURE strikes me as drawing conclusions that were known 50 years ago or conclusions that are conceptually trivial. In my biased opinion a good experiment advances the subject much more than meta-analyses. Part of my concern is that meta-analyses scramble apples and oranges without knowing it, and that ecological wisdom is more likely to be useful at the local level rather than a potpourri of global levels. The basic problem is that we do not know the scale of generality of our results.

I have not yet seen an insider paper on "the truth behind meta-analyses". Who could be the whistle-blower?

10. Generality is the goal of all sciences. In ecology we might achieve generality at the local level, possibly only at the population level, and only when the number of ecologists in the world exceeds the number of lawyers and the budget for ecological research exceeds that of the military.

Ecology has progressed through the *Era of Global Generality* in the 1950s, 1960s and possibly the 1970s, when models were clear, data were few, and ecological champions ruled ("it is not customary to question the statements of the Professor..."). The *Era of Local Generality* perhaps occupied part of the 1970s, the 1980s and part of the 1990s when generality was thought to be more local in the geographic sense ("This hypothesis applied only in areas of winter snow cover") or in the taxonomic sense ("This plant defense hypothesis applies only to long-lived woody plants"). By 2000 we were well into the *Era of Ecological Chaos* in which detailed studies of partial food webs seemed to invalidate every ecological generalization or 'law' so that generality seemed ever farther from view. What will happen next is never clear, but I might suspect we are in some kind of a long-term cycle that will swing back again from chaos.

I suspect that much ecological strife has arisen because of a failure to apply the experimental method and for competing schools to agree on what a defining experiment is and how it should be conducted. Problems of this sort are not solved by meta-analyses but they could be assisted by serious discussions of what particular experiments demonstrate and what the defining hypotheses are for any particular subdiscipline of ecology. I think we press on, do our best, and realize that no one person knows the truth, and dangerous ideas are desirable. That is the essence of scientific progress.

Acknowledgements

I thank the reviewers for their comments. They should not be held responsible for my errors of commission or omission.

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